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## Distribution of Progeny by *Chelonus texanus* Cress. (Hymenoptera: Braconidae)

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### Introduction

The efficiency of an entomophagous parasite may be defined as the capacity which it possesses for distributing its eggs among the available host population in such a manner that its progeny have the best possible chance of survival. This capacity is determined by a number of factors which are, as yet, imperfectly understood. Among these factors are the ability of the parasite female to discriminate between hosts which are suitable for the development of her progeny and those which are not; the relative densities of the parasite and host populations; the habits of the host insect; and the behaviour of the parasite itself during oviposition.

Host insects may be divided into a number of groups according to whether they are normally stationary, active, exposed or protected from parasite attack and according to the nature of their distribution over a given area. Each group presents a specific problem in relation to the parasite which attacks it. Similarly, parasites may be classified on the basis of their behaviour during oviposition, i.e., according to (1) whether the host is paralysed before use or not; (2) whether one or more eggs are normally deposited and can develop to produce adults on one host individual; (3) the degree of development of the discriminative ability of the parasite female.

A tentative classification of hosts based on these lines would be somewhat as follows:

GROUP I. Hosts moving in exposed situations (e.g., on leaves of plant or surface of medium); not paralysed by parasite before oviposition; host active.

Example: *Plutella maculipennis* Curt. and its parasite *Angitia* sp.

GROUP II. Hosts moving but are paralysed by parasite before oviposition; hosts usually found in protected situations such as burrows in stems.

Example: *Heliothis armigera* Hbn. in the ears of corn and its parasite *Microbracon brevicornis* Wesm.

GROUP III. Hosts stationary (e.g., eggs, pupae and prepupae) and more or less exposed to attack (on leaves of plants etc.). This group may be subdivided into

A. Host exposed and readily accessible to examination by the parasite, e.g., eggs.

B. Host enclosed in a protective covering through which it must be examined by parasite, e.g., pupa in a cocoon. The host may or may not be paralysed before oviposition.

GROUP IV. Hosts in protected situations and not in direct contact with the parasites (e.g., in burrows in stems of plants); not paralysed by parasite before oviposition.

A. Parasite oviposits through protective wall.
Example: *Cephus pygmaeus* L. and its parasite *Collyria calcitrator* Grav.

B. Parasite enters micro-environment to find the host.
Example: *Apanteles sesamiae* Cam. which enters the burrows of its host, *Busseola fusca* Hmpn. in maize plants.

GROUP V. Oviposition by parasite not directly on the host but eggs or larvae deposited on the substratum.

A. Ova of parasite ingested by host; or the parasite larvae are encountered by the host by chance.

B. Parasite larvae active and search for hosts.
Examples of this group are found among the Tachinidae.

The above is not to be regarded as a complete classification. It is obvious that a number of variations can be added thereto in order to make it more comprehensive. The point which it is intended to emphasize here is that a wide variation exists in the relationship of parasite to host and that the opportunity which is afforded the former for the examination of the host prior to oviposition is governed by the habits of the host. Thus, in some groups this opportunity is offered freely, as in the case of the stationary eggs of Group I. In others it is reduced to a minimum; while in Group V it is entirely absent.

It seems evident that the relative habits of hosts and parasites will have a marked influence upon the practical outcome of any discriminative faculty that may be possessed by an ovipositing female parasite. For example, a stationary host, such as the egg of a moth, provided that it is in an exposed situation, is more accessible for an intensive examination prior to its use than is an active larva of the same insect. Provided other conditions are equal, it might be expected that superparasitism, with its concomitant wastage of progeny, will be less likely to occur in the former than in the latter case.

While the possession of a discriminative faculty seems to be fairly general among parasitic Hymenoptera, it would appear that there is considerable variation in the development or exercise of the ability to distinguish between suitable and unsuitable (i.e., parasitized and unparasitized) hosts among the different types of parasites and that much investigational work remains to be done, both in field and laboratory, before the subject can be discussed adequately. Superparasitism is the phenomenon which indicates a breakdown in the faculty. Some of the various factors which appear to govern this breakdown in the field have been discussed by the present writer (Ullyett, 1943) in the case of *Angitia* sp. which attacks the active larva of *Plutella maculipennis* Curt., in South Africa. Superparasitism could be correlated with the host density, the degree of parasitism of the host, with the host/parasite ratio per unit area and with quantitative changes in the environment. It is hoped to study these factors more exactly as opportunity offers.

The sum total of the effects of the factors mentioned above is reflected in the efficiency with which the parasite distributes its progeny among the available host population. The crux of the problem therefore lies in the degree of development of the discriminative faculty and upon its modification by environmental conditions. Two contrasting cases have now been subjected to experimental

treatment. In a previous paper (Ullyett, 1945), the manner in which the progeny of the Braconid, *Microbracon hebetor* Say, are distributed among larvae of the flour moth, *Ephestia kühniella* Zell., was described. This corresponds to Group II above, where the active host is immobilized before being used for oviposition and where the parasite progeny develop externally on the paralysed larva. More than one parasite can develop from a single host individual. The female can examine the host thoroughly before accepting it as suitable for oviposition. The search for hosts was shown to occur in two distinct phases.

The present paper deals with a case from Group I, in which the host is exposed and is stationary, thus giving the parasite the maximum opportunity for examination. On comparison with *Microbracon,* therefore, the main difference in conditions is the initial activity of the host insect and therefore in the difficulties of search for host material.

## Material and Methods

The subject of the present experiments is the Braconid, *Chelonus texanus* Cress. This is an important larval parasite of a number of major lepidopterous pests in the Americas. Among these are *Heliothis armigera* Hbn., *Loxostege sticticalis* L., and species of *Laphygma.* The parasite has been introduced into South Africa for liberation against *Loxostege frustalis* Walk., the larvae of which at times constitute a serious menace to the Karroo bushes (*Pentzia* spp.) which are a valuable feed for sheep in an area where very little else grows during the greater part of the year.

Large-scale laboratory rearing of *Chelonus* is carried out with *Ephestia kühniella* as host. Although *Ephestia* is not normally attacked in nature, the parasite readily propagates on it in captivity and will develop normally thereon. As with other members of the same sub-family, *Chelonus* oviposits in the egg of its host. The latter must be in a suitable stage of embryonic development so that the parasite egg can be deposited within the body of the larval embryo. The egg hatches only after eclosion of the host larva and *Chelonus* is therefore a true larval parasite.

The host/parasite relationships are as follows: The host is stationary and freely exposed to attack. Only one parasite larva can develop to maturity in each host so that superparasitism occurs when more than one egg is deposited in a host egg. The parasite female has ample opportunity for an examination of the host and its efficiency will therefore primarily depend upon its ability to distinguish between unparasitized and suitable hosts and those which have been parasitized or are otherwise unsuitable. The relationship between host and parasite is therefore similar to that which occurs in the case of a true egg parasite.

In the present instance, however, the host egg is suitable as a host only towards the end of the incubation period; whereas it can be used successfully by an egg parasite only for a restricted time at the beginning of the period. In the experiments about to be described, host eggs were used when approximately twenty-four hours old. At this time, under the conditions obtaining, they had attained the necessary stage in development and the embryo was fully formed.

The cages used in the experiments were either Syracuse watch-glasses or petri dishes. The former were found more convenient in all but a few cases. Host eggs were arranged on a circle of squared paper (1-inch squares divided into tenths) cut to fit the dish, the general scheme being shown in figure 1. At the outset, the question arose as to whether the hosts should be

scattered at random over the area or whether they could be arranged in a more systematic manner. A preliminary test was therefore made to ascertain whether any difference in results could be expected between the two methods.

In this test one hundred host eggs were used per parasite female in each series. In series A the eggs were arranged in a large square in the centre of a watch glass in a systematic manner. In series B the hundred hosts were scattered at random over the surface of the paper disc. A single female was put into each dish. In each case the female was twenty-four hours old and had been mated but had not yet oviposited. Six replications of each series gave the following significant means: Series A—83.6 percent and Series B—82.8 percent effective parasitism. There was no significant difference between these two means and it was accordingly concluded that the method by which hosts were distributed in experimental cages made no difference to the manner in which the parasite progeny were distributed. Because of its greater convenience in keeping a check on the host eggs during subsequent dissection, the systematic arrangement was adopted for experimental work.

In all the series described hereunder, the female parasites used had not previously oviposited. After emergence, they were kept for twenty-four hours, during which time they were fed and mated. They were then transferred to the experimental cages with hosts for a further twenty-four hours and then removed and placed with the general breeding stock. Experiments were normally conducted at a constant temperature of 80 degrees F. and in daylight. There were six replications of each experiment, it being found that this was sufficient to give statistically satisfactory results.

## The Effect of Host Density

Series of from twenty to two hundred host eggs were arranged in Syracuse watch glasses and stuck on to the squared paper within or around the central one-inch square, each egg being placed in one of the small squares (figure 1). Parasite females of the same age and newly fed and mated were placed singly in each of the cages. At the end of the period allowed for oviposition, the host eggs were dissected and the number of parasite eggs found therein recorded.

Two aspects of the effect of varying the density of the host population per unit area are important from a practical point of view. These are (1) the effect on the general utilisation of the hosts by the parasite (i.e. the percentage of the host population destroyed) and hence on the efficiency with which the host can be controlled at any given time; (2) the efficiency with which the parasite female distributes her eggs among the available host material which will govern the degree of success it will attain in the maintenance of its own population at a high level.

### (a) *The effect on host utilisation*

During the period of the experiment, the total number of hosts found and parasitized by the female *Chelonus* rapidly increased as the host density became greater. This is illustrated in figure 2. At the same time, the *proportion* of the available host population found and used by the parasite gradually diminished as the numbers of hosts available increased (figure 3). This is readily understood if the finding of the hosts by the parasite is regarded as a function of the time available for searching the given area which, in the experiments, was strictly limited.

It is possible that the parasite was not able to *find* all the hosts within the experimental area during the time allowed, even when the original number of

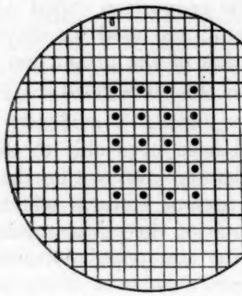

FIG. 1

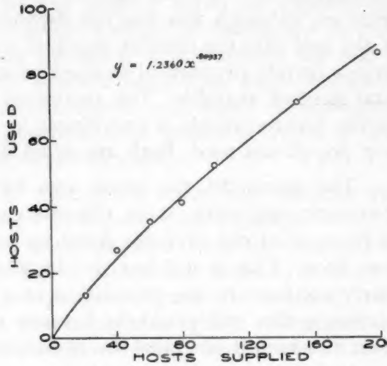


FIG. 2

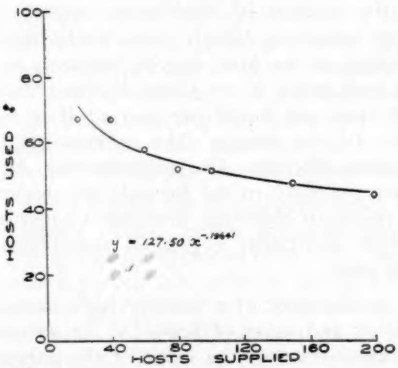


FIG. 3

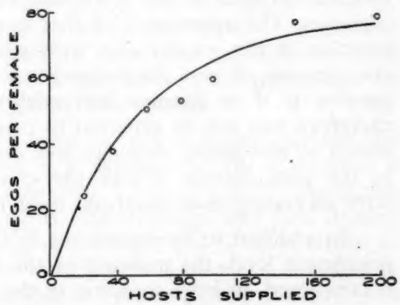


FIG. 4

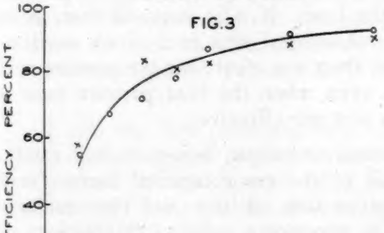


FIG. 5

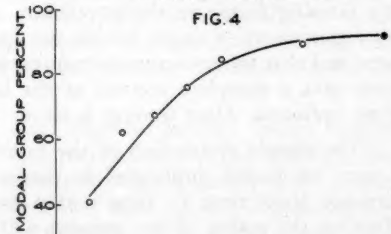


FIG. 6

FIG. 1. Arrangement of *Ephestia* eggs on squared paper for use with *Chelonus* females.

FIG. 2. *Chelonus texanus*: effect of host density on total number of eggs used.

FIG. 3. *Chelonus texanus*: effect of host density on proportion of host population used during twenty-four hours.

FIG. 4. *Chelonus texanus*: effect of host density on the number of eggs deposited per parasite female.

FIG. 5. *Chelonus texanus*: efficiency of females in the distribution of progeny at different host densities. o=systematic distribution of hosts as in fig. 1. x=random distribution of hosts.

FIG. 6. *Chelonus texanus*: percentage of hosts falling in the modal group at different host densities.

available hosts was equivalent to the number actually found at the higher host densities, although this was not demonstrated by the experimental data. In spite of the fact that the number supplied could have been found within the specified time, a certain proportion escaped parasitism and the proportion varied with the total number available. The regression of hosts found and used for oviposition on the hosts available is curvilinear in form, as is that of the proportion of the host population used. Both are fitted with curves of the same general type.

The search of the given area by the parasite female is evidently not a systematic one since, were this the case, it should have been able to discover all or most of the available hosts up to a certain density level within the given time limit. This it did not do. In fact, the data present features which most nearly conform to the postulation of a random search of the environment. This random action will gradually become replaced, as the host population nears the point at which it saturates the environment, by simple movement of the parasite female from one host to another—a procedure which cannot be called a search in the strict sense of the term. Although this does not necessarily mean that hosts are no longer *visited* at random, the element of randomness appears to become reduced so that it is replaced by something which gives results intermediate between it and systematic searching as the host density per unit area increases. The appearance of this in the final result is no doubt due to a combination of the greater ease with which hosts are found per unit of time and the exercise of the discriminative ability of the female. The actions of the parasite tend to become increasingly more efficient. The experimental data, therefore, can not be expected to conform precisely to the formula for random search at any point, although this may represent the basic principle concerned in the phenomenon. Under the conditions described, a gradual modification with increasing host numbers, must take place.

In addition to its importance in the maintenance of a suitably high parasite population level, the question of the finding and using of hosts by the parasite is concerned, in large measure, in the determination of the value of the parasite as a limiting factor in the population of the hosts. If it is assumed that, as in the experiments, a single female occupies one unit of area in a given environment and that other factors remain constant, then it is clear that the parasite will never give a complete control of the host, even when the host/parasite ratio is at an optimum. Host finding is never 100 percent effective.

The simple abstraction of the experimental technique, however, will rarely, if ever, be found duplicated in nature. All of the environmental factors will fluctuate from time to time within any given unit of area and the resultant effect on the action of the parasite will be to produce a series of fluctuations in its efficiency as a controlling agent, i.e., in its ability to find and destroy hosts. The majority of these environmental changes are unpredictable and it therefore follows that the success of a parasite in controlling its host cannot be foretold with any degree of accuracy. Any statement on these lines must necessarily be merely the expression of an opinion and not the statement of a scientific conclusion.

(b) *Effect on distribution of progeny*

The relationship between host density and host finding has a close bearing on the manner in which the parasite female distributes her eggs among the available hosts. There is a highly significant positive correlation between the total number of eggs deposited by the parasite within a given time and the density

of the host population per unit area. In the present series of experimental females $\tau = +.9575$ and $P < .01$. The number of eggs laid during the twenty-four hour period increases fairly rapidly at the lower host densities, the rate of increase gradually diminishing as the daily possible number of eggs per female is approached. The relationship is hence a curvilinear one which is represented most nearly by a curve of the simple exponential type shown in figure 4. This gives a satisfactory approximation to the observed data.

The comparatively low production of eggs at the lower host densities may be ascribed to the increased proportion of the total time available which is occupied with unproductive search of the environmental unit, accompanied by the exercise, by the parasite, of a certain degree of restraint from oviposition in previously-parasitized hosts. The latter factor presupposes the existence of a discriminative ability on the part of the female parasite which will enable her to distinguish between parasitized and unparasitized hosts. That such a faculty is present in *Chelonus* will become clear.

The most significant effect of the density of the host population on parasitism is in the actual distribution of the parasite eggs laid among the available hosts. Since only one parasite larva can develop to maturity in each host individual, only one egg of those deposited in each parasitized host egg is effective. The relative efficiency of a female parasite in producing viable progeny and hence in maintaining or increasing the parasite population at different host concentrations, may therefore be expressed as the number or percentage of "effective eggs" per female for the twenty-four hour period.

The figures for the present series have been plotted in figure 5 where the efficiency of the female in distributing her eggs among the available hosts is expressed as a percentage of the total eggs deposited. There is a highly significant positive correlation between the percentage of effective eggs and host density ($\tau = +.9213$; $P < .01$). The observational data are plotted as open circles in the figure. A parallel series, in which hosts were scattered over the unit area at random, is indicated by crosses. It is evident that there is no significant difference between the two series and that they are both equally well represented by one and the same curve. The efficiency of the females was therefore not influenced by the manner in which the hosts were distributed over the experimental unit area.

From the data presented here, it is clear that the parasite female does not distribute her eggs at random among the host population. On the contrary, there is evidence of the exercise of a well-developed discriminative ability which enables the female parasite to distinguish between hosts already containing parasite eggs from those which are still unparasitized. This ability, however, is modified by the number of hosts which are made available to the parasite within the given area and during the given period of time. Notwithstanding this, the general tendency throughout the series was for the female to distribute her eggs among the hosts found so that the resultant progeny would have the optimum chance of survival. This happened even under the most adverse conditions of host density provided in the experiment. This well-marked tendency is most clearly seen when the results are arranged in the form of a frequency distribution showing the number of hosts containing 1, 2, 3, ..........n, eggs each. This is done in Table I.

In all the series, without exception, the modal group was that in which one egg per host individual was the rule. With the exception of Series A, which contained the lowest number of hosts, the majority of parasite eggs were

deposited singly in the hosts used. The proportion of hosts which fell within the modal group is plotted in figure 6 for the complete series. This offers a measure of the effect of host density per unit area upon the discriminative ability of the parasite female. The proportion of hosts containing only one parasite egg per individual (= 100% efficiency) increases in direct proportion to an increase in the number of hosts present, at first fairly rapidly and then more gradually as the host individuals per unit area approach the optimum density for parasite activity under the conditions of the experiment. The *efficiency* of the parasite in the distribution of its progeny is therefore determined primarily by the possession by the female of an inherent discriminative faculty which, however, becomes modified in a regular manner by the degree of opportunity which is afforded for its exercise in the choice of suitable hosts.

TABLE I

*Chelonus texanus:* Frequency distribution of progeny by single females at different host densities.

| Eggs per host | f = no. of hosts in series | | | | | | |
|---|---|---|---|---|---|---|---|
| | A (20) | B (40) | C (60) | D (80) | E (100) | F (150) | G (200) |
| 1 | 29 | 80 | 118 | 171 | 226 | 388 | 278 |
| 2 | 13 | 33 | 37 | 41 | 36 | 35 | 19 |
| 3 | 9 | 14 | 14 | 11 | 3 | 6 | .. |
| 4 | 8 | 2 | 2 | 2 | 1 | .. | .. |
| 5 | 4 | 1 | 2 | .. | .. | .. | .. |
| 6 | 2 | .. | .. | .. | .. | .. | .. |
| 7 | 2 | .. | .. | .. | .. | .. | .. |
| 8 | 1 | .. | .. | .. | .. | .. | .. |
| Total hosts | 68 | 130 | 173 | 225 | 266 | 429 | 297 |
| Mean Eggs per Host | 2.47 | 1.55 | 1.46 | 1.31 | 1.16 | 1.11 | 1.06 |

### The Effect of Parasite Density

A series of tests was made in which the number of female parasites per unit area was varied, the area itself and the number of host eggs contained within it being maintained constant. The general experimental conditions were as before. In the case of single females per unit area optimum conditions for oviposition were realized when there were approximately one hundred and fifty host eggs in the given area. This number was used in the present series. The number of females placed in each container varied from one to six. There were six replications of the experiment and the exposure time was twenty-four hours.

(a) *Effect on host utilization*

The number of hosts found and parasitized by the female parasites during the twenty-four hour period increased as the number of parasites per unit area

was increased. This continued up to the point at which between three and four females were present together in the environment. After this, the number of hosts attacked commenced to decline. This is shown in the top curve in figure 7. The curve first ascends, then flattens out and finally turns over and commences to descend.

Thus, with a constant number of hosts per unit area and with a limited period of time, there is a point at which the density of the parasite population is at an optimum for the destruction, and hence the control, of the host population. Beyond this point, any addition to the parasite population decreases its efficiency as a whole in this respect and the absolute number of hosts which survive increases. The reason for this phenomenon is not clearly demonstrated by the experiment. It has previously been ascribed to either competition between parasite females for the limited area over which the hosts are distributed or to the interference with oviposition occasioned by the frequent contacts between searching and ovipositing females. These two aspects, however, are obviously so closely related to one another that it is almost impossible to separate them, since "competition for space" clearly leads to more frequent contacts between individuals within a given area as it becomes more severe.

Although the above is true of the total number of hosts attacked by the parasite population as a whole, the number of hosts which is attacked per female parasite shows a different picture. The number steadily declines with increasing parasite density as is shown by the bottom curve of figure 7. This happens in spite of the fact that there is always a fairly large proportion of the host population which remains unparasitized at the end of the time allowed in the experiment. The adverse effect of increasing the parasite numbers per unit area therefore occurs even when only one additional female is introduced into the area. At this stage it can hardly be said that the environment is overcrowded, so that the explanations offered above are difficult to accept here. It is necessary to examine the problem from another angle in order to obtain a satisfactory answer to the question. This will be done after other general effects of increasing parasite density have been described.

(b) *Effect on oviposition*

The increase and decline in the number of hosts used by the total parasite population with increasing parasite density is reflected in the total number of eggs deposited by the females per twenty-four hours. The curve showing this (figure 8A) has the same general form as in the case of the total hosts used (figure 7). Similarly, the number of eggs laid by each female during the period shows a close relationship to the number of hosts used per female (figure 8A and figure 7). In the former case, the data can be fitted satisfactorily with a linear regression line.

The increasing parasite population per unit area, acting as a whole, therefore exhibits an increase in efficiency up to an optimum density level, after which its capability, both in controlling the host and in the production of eggs, diminishes with successive increments in numbers. But while the total production of eggs by the population thus increases rapidly during the pre-optimal stage, the capacity of individual females in the population shows a steady decline throughout. Hence, the population *per se* gains while the individual loses by the increase in population mass.

(c) *Effect on distribution of eggs*

The ultimate test of efficiency on the part of the parasite, however, lies in the manner in which the eggs produced are distributed among the host indivi-

duals. For the present series this is shown by the frequency distribution in Table II. The modal group in all cases is that in which one egg is deposited in each host attacked, indicating the continued exercise throughout the series of the discriminative ability shown by the single females. Here, as before, there is a strong tendency for the females to distribute their eggs so that the resulting progeny have the best chance of survival. This tendency is modified, as a population attribute, by the increase in parasite density, as is shown by the curve depicting the proportion of hosts falling into the modal group at various parasite concentrations. This progressively decreases as the parasite population becomes greater. (*vide* figure 9).

TABLE II

*Chelonus texanus:* Frequency distribution of eggs in hosts with varying female parasite density per unit area, the hosts remaining constant.

| Eggs per host | f = no. of hosts. | | | | | |
|---|---|---|---|---|---|---|
| | number of females: | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 |
| 1 | 153 | 205 | 218 | 186 | 190 | 154 |
| 2 | 20 | 59 | 109 | 119 | 119 | 115 |
| 3 | .. | 3 | 23 | 37 | 31 | 45 |
| 4 | .. | 2 | 3 | 10 | 10 | 9 |
| 5 | .. | .. | .. | 2 | 2 | 2 |
| 6 | .. | .. | .. | 1 | .. | 2 |
| Total hosts | 173 | 269 | 353 | 355 | 352 | 327 |
| Mean eggs per host | 1.12 | 1.26 | 1.47 | 1.67 | 1.62 | 1.77 |

Since only one parasite egg can give rise to mature progeny in each host individual, and since both the number of hosts attacked and the total eggs laid are related to parasite density in a very definite manner, the total number of eggs which will be effective in giving rise to progeny will vary with these two factors. That this is so is clearly shown on plotting the experimental data. In figure 8, curve C shows the effective eggs for the whole of the parasite population at varying densities per unit area. It is to be noted that, after a certain point, an increase in the total number of eggs laid (curve A) is not accompanied by any corresponding rise in the number of effective eggs. After this particular density level is reached, therefore, it may be said that any further additions, although giving rise to an increase in total egg production, merely result in an increase in the number of wasted eggs produced.

The number of effective eggs produced per female parasite is lower than, but closely related to, the total eggs produced per female (figure 8, B & D). As noted for the total eggs, there is a steady decrease in numbers as the parasite density increases, this decrease being represented by a highly significant linear

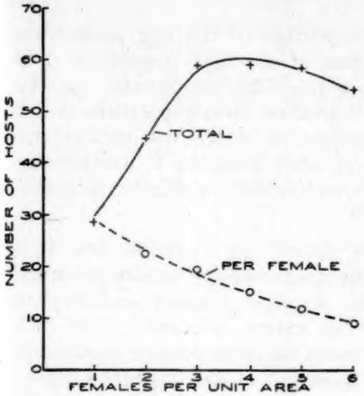


FIG. 7

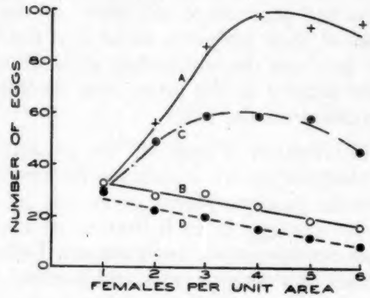


FIG. 8

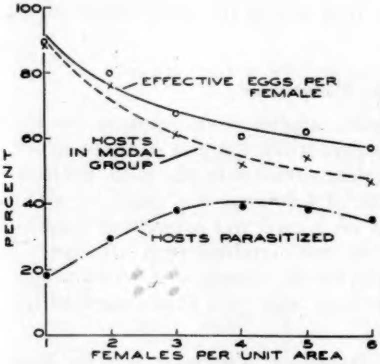


FIG. 9

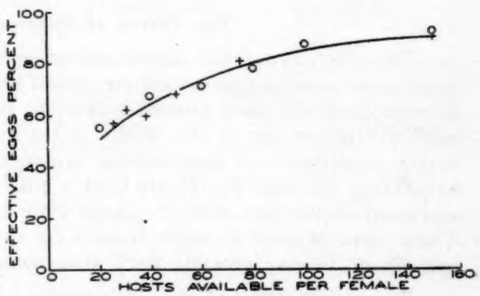


FIG. 10

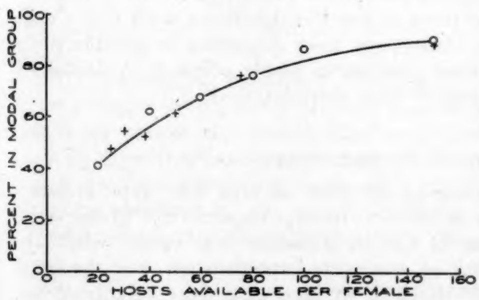


FIG. 11

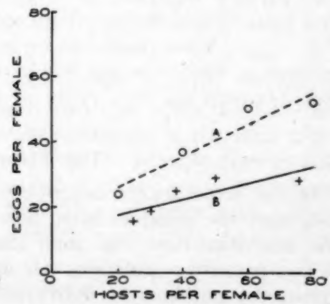


FIG. 12

FIG. 7. *Chelonus texanus*: the effect of varying parasite density on the total number of hosts parasitized and on the number parasitized per female.

FIG. 8. *Chelonus texanus*: the effect of parasite density on the number of eggs produced. A, total eggs for the population; B, total eggs per female; C, total effective eggs; D, effective eggs per female.

FIG. 9. *Chelonus texanus*: effect of parasite density on the percentage of hosts parasitized. The percentage of hosts in the modal group is also shown.

FIG. 10. *Chelonus texanus*: effective eggs percent from the varied parasite density series plotted against the number of hosts available per female. Data from single females is plotted on the same curve. x=data from the parasite density series; o=data from single females.

FIG. 11. *Chelonus texanus*: effect of parasite density as shown when the percentage of hosts falling in the modal group is plotted against the number of hosts available per female. x=parasite density data; o=single females.

FIG. 12. *Chelonns texanus*: regression of number of eggs per female on hosts available per female. A in single female series, B in parasite density series.

regression of eggs on parasite density. The proportion of the egg production which is effective closely follows the proportion of the host population used which falls into the modal group (*vide* figure 9). This proportion may be regarded as the percentage efficiency of the individual female parasites in the distribution of their progeny, since it is the proportion which will survive and eventually produce the succeeding generation of adult parasites. It decreases as the parasite density in the given area increases and exhibits a significant curvilinear regression on the latter.

The distribution of eggs by the parasite is clearly not a random one. It is however, modified by environmental factors. The discriminative faculty possessed by the female parasite which gives rise to the strongly marked tendency to deposit only one egg in each host is, to a certain extent, affected by the host and parasite densities in the environment. Even under the most adverse conditions, however, this tendency persists and is clearly indicated in the frequency distributions presented above. This ability and, in particular, its resistance to modification by external factors, is clearly an important factor in determining the value of a given parasite in the control of its host and in the stabilization of its own population.

## The Effect of Previous Parasitism

The exercise of the discriminative faculty implies a recognition by the parasite not only of eggs which she herself has parasitized but also of those which have received the prior attention of other female parasites in the same environment. A further test of this ability in the case of *Chelonus* was made by alternating parasitized and unparasitized host eggs on a card and presenting them to ovipositing females. Each card had a total of one hundred eggs arranged as described earlier and half of which were known to contain one parasite egg. These were exposed to single females for one hour and were then examined for parasitism. Twelve separate tests were made.

The results showed that an average of seventeen eggs were laid by each female parasite. Of these, six were laid in parasitized hosts and eleven in unparasitized hosts. The difference between these means was significant with $t = 2.1542$ and $P < .05$. Thus nearly twice as many eggs were deposited in suitable hosts as in hosts in which the egg would never give rise to viable progeny. A deliberate choice between the two types of host is thus demonstrated.

## The Effect of Varying Area

In the experiments described above, the unit of area was kept constant throughout, the variables being host or parasite density, respectively. In the series to be described now, the total area of the environment was varied while the host and parasite populations *per unit of area* were kept constant. For the latter purpose, the numbers of individuals allocated in each case were calculated per square centimetre and were based upon the optimum class in the previous experiments. Varying area was obtained by using petri dishes of different diameters.

In each series of dishes there was a constant host population of 6.9 per sq. cm. which was equivalent to the density in the previous experiment where one hundred and fifty hosts were supplied in Syracuse watch glasses to single females. The parasite population was maintained at a density of one individual per 5.4 sq. cm. The figures were approximated to the nearest whole number, giving the following numbers per series:

| Series No. | Area Sq. Cm. | No. of Hosts | No. of Females |
|---|---|---|---|
| 1 | 17.06 | 118 | 3 |
| 2 | 21.73 | 150 | 4 |
| 3 | 40.26 | 278 | 7 |
| 4 | 64.18 | 443 | 12 |
| 5 | 146.98 | 1014 | 27 |

The exposure of hosts to parasites was for twenty-four hours under conditions as for previous experiments. Dissections were carried out at the end of this period and records kept as before. Results are summarized in Table III.

TABLE III

*Chelonus texanus:* Effect of varying total environmental area on distribution of progeny.

| Series No. | Area Sq. Cm. | Hosts attacked per Female | Percent Hosts in modal Group | Eggs per Female | Effective Eggs Percent |
|---|---|---|---|---|---|
| 1 | 17.06 | 14 | 65 | 14 | 36 |
| 2 | 21.73 | 17 | 53 | 17 | 44 |
| 3 | 40.26 | 18 | 55 | 18 | 46 |
| 4 | 64.18 | 17 | 52 | 16 | 45 |
| 5 | 146.98 | 17 | 50 | 17 | 46 |

There was no significant difference between any of the five different series in the results shown in the table. It is clear, therefore, that when the host/parasite ratio per unit of area is maintained as a constant, variations in the total area over which these populations are spread and over which the parasite females have to roam in their search for hosts, have no significant effect upon the degree of control exercised by the parasite over the host. The efficiency with which the parasite distributes its progeny among the available hosts is also unaffected.

**The Host/Parasite Ratio**

In the experiments dealing with varying parasite density per unit area, the number of hosts supplied in that area was kept constant. The same absolute number of hosts was therefore available to each different population of parasites. This procedure introduced what is technically an error into the experimental method, since it produced an additional variable over and above that of varying parasite density. This hidden variable is the ratio between the numbers of hosts and parasites within the given area. This changed as the parasite population was increased so that the host/parasite ratio became less with each succeeding increment in the parasite population.

This technical error is present in much of the work which has been published to date on this subject and its implications do not seem to have been fully realized. It is clear, from the available experimental data that the host/parasite ratio is an important factor in determining the success of a parasite in the control of its host. Up to a certain point, the efficiency of the parasite in this respect, as well as in the more advantageous distribution of its progeny, increases as more and more hosts become available to it within the environment. In the present instance, the increase in parasite density in the experimental series is inevitably accompanied by a decrease in the ratio of hosts to parasites and therefore there is a progressive deterioration in one of the most important factors governing parasite activity.

The effect of this factor is mixed up with the direct effect of the increase in density of the parasite population and it is difficult to separate them sufficiently to be able accurately to assess their relative importance in producing the phenomena observed. Further careful and extended experimental treatment is necessary in order to be able to do this. An attempt will be made, however, to analyse the data available since this aspect of the problem is important from a practical point of view.

The data for the series in which parasite density was varied were recast so that the independent variable was the number of hosts supplied per female parasite per unit area. They were then plotted in the new form and the observational points from the relevant single female series were plotted on the same graph. When this was done for each aspect of the problem, the following points became evident.

(1) The percentage of eggs deposited by female parasites which is *effective* is always dependent upon the number of hosts available per female and is the same, whether one or more parasites are present in the given area, provided the host/parasite ratio remains constant (*vide* figure 10). From this, it is clear that an increase in parasite density per unit area does not affect the basic efficiency with which the parasite female distributes her progeny, i.e., it does not modify the discriminative ability of the female in any obvious manner. As in the single female series, modification of this faculty is produced only by variations in the ratio of hosts to parasites present in the environment. As this ratio falls, efficiency becomes impaired.

(2) This strong tendency on the part of the parasite to create optimum conditions for the development of its progeny persists even when the number of parasites per unit area is increased to an adverse extent. It is further demonstrated by the percentage of hosts which fall into the modal group of the frequency distribution. In this, the data from the varied parasite density series agree almost perfectly with those from the single female series where the host/parasite ratio is the same (*vide* figure 11). Hence there is no evident effect of parasite density on the efficiency with which the hosts available were utilized for depositing the eggs laid during the experimental period.

(3) On the other hand, the total number of eggs deposited per female during twenty-four hours where more than one parasite is present in the given environment differs widely from the number deposited by single females at an equivalent host/parasite ratio. It is always much lower in the former case (*vide* figure 12). Only at the extremes do the two curves approximate. It is evident that, where more than one parasite is present, the addition of more hosts per female to the environment will not make as much difference to the total number of eggs

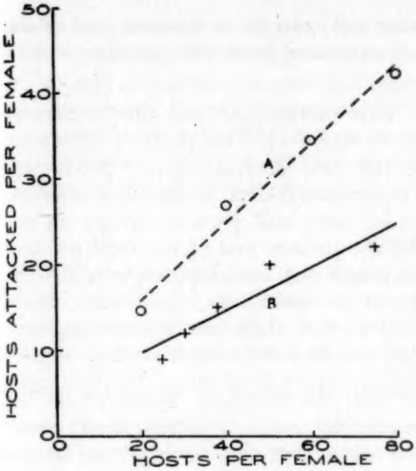


FIG. 13

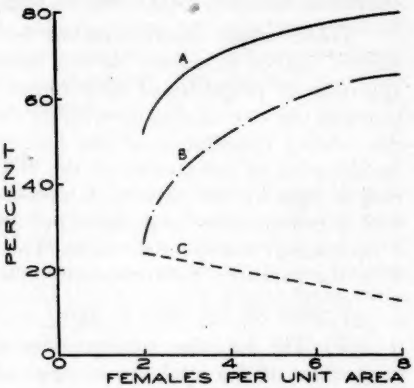


FIG. 14

FIG. 13. *Chelonus texanus*: regression of the number of hosts attacked per female on the hosts available per female, A in single female series, B in parasite density series.

FIG. 14. *Chelonus texanus*: percentage loss in eggs in the series with varying parasite density. A, total loss; B, loss due to unfavorable host/parasite ratio; C, loss due to increasing parasite density.

produced by the parasite population as it did in the case of single females, although some improvement will be effected by so doing. There is, here, a direct and definite effect of increasing parasite density as opposed to the effect which can be ascribed to the host/parasite ratio.

(4) The total number of hosts parasitized by each female is also much less in the series with varied parasite density. As might be expected from the egg distribution data, this shows a relationship to the host/parasite ratio and to the results of the single female series which is very similar to that in the case of total eggs described above (*vide* figure 13). There is an appreciable difference between the two series, indicating the presence of some interference factor which reduces oviposition in individual females when more than one parasite inhabit the environment.

**Relative Importance of the Factors**

A further analysis of the data can be made by taking the results obtained from the single females at each different host/parasite ratio as representing the maximum efficiency which can be attained by the parasite under those conditions and as reflecting the effect of the variations in this ratio alone. Then the difference between any point on the regression line for these observations and any corresponding point on the line representing the series having a varying parasite density (*vide* figure 12) will give a measure of the extra loss due to the factor or factors induced by the increase in parasite density per unit area.

This difference may be expressed as a percentage of the total loss of eggs due to all factors. This latter figure is determined by taking as a maximum the results observed at the optimum ratio of hosts to parasites in the single female series. This was attained, approximately, when one hundred and fifty hosts were available per female parasite and when the parasite deposited, on an average, a total of seventy-four eggs during the twenty-four hour period as read on the curve.

The effect of altering the host/parasite ratio can be ascertained in a similar manner from the single female series and variations from the optimum can be expressed as a percentage loss of eggs.

These simple transformations have been carried out and the results are plotted against increasing parasite density in figure 14. This diagram shows the approximate proportional distribution of the total decrease in egg production between the two factors involved in the experimental data. It therefore indicates the relative importance of the host/parasite ratio and parasite density in the modification of the control of the host by the parasite and of the total production of eggs by the parasite. It should be noted that increasing parasite density with a constant host population per unit area, as used in the experiments, means a decreasing host/parasite ratio. The two factors therefore operate together with the parasite's discriminative ability to produce the results as they appear.

A study of the chart in figure 14 indicates the following significant points:

(1) The loss due to increasing density, *per se*, is a comparatively small proportion of the total loss of eggs when taken over the whole series. At the lower parasite densities, however, it represents a considerable proportion of this loss. For example, when two parasites are present in the area, the loss due to this factor is approximately half of the total loss, i.e., it is equivalent to that occasioned by the decreased host/parasite ratio.

(2) As the parasite density is increased, the proportion of the total loss due to an unfavorable host/parasite ratio increases rapidly while the proportion due to the increasing parasite population per unit area decreases gradually. At first sight, the decrease in the effect of a factor with increase in the intensity of the factor itself appears remarkable. This is clearly due to the fact that, as parasite density is increased, the host/parasite ratio becomes more and more unfavorable to the parasite and its influence upon the activity of the females becomes more and more important so that, in effect, it becomes the factor which dominates the situation and the relative importance of parasite density wanes. It should be remembered that the data illustrated in the chart are *proportional* and that the *absolute* effect of parasite density increases as the factor itself is intensified (cf. figure 12). Because of this decrease in proportional representation, the curve for total loss in egg production per female reflects the curvilinear relationship to parasite density per unit area which is shown by the host/parasite ratio and this curve is little affected by the very gently-sloping linear relationship of the effect of parasite density itself.

(3) The linear regression produced by the parasite density factor seems to indicate that this factor is, at least in part, mechanical in nature and is not density-dependent so far as the host is concerned. The progression which results from adding to the intensity of the factor is arithmetical in character and the variation observed occurs relative to the absolute density of the parasite population and has nothing to do with the density of the host population.

The factors which have been suggested as the explanation of the phenomenon (*vide* De Bach and Smith, 1947) might produce such a result but this will depend, to a large extent, upon the nature of searching activities on the part of the parasite population. Thus, if searching is at random, then the frequency of contacts between individual parasites within the environment will depend upon the laws of chance. The resulting curve should be of the type associated with the theory of probability, i.e., it would not be a straight line but would most probably be of the exponential type. Similarly, "competition for space"

would be governed mainly by the law of diminishing returns and would not result in a linear relationship with increasing density.

Observations have shown that searching for hosts and the distribution of progeny among them are not random phenomena, although some evidence of randomness may exist. The analysis given above provides an additional evidence of non-random activity in the search of the environment, provided that the most likely explanations of the phenomena are accepted.

## Discussion

Under optimum environmental conditions, *Chelonus* exhibits a high degree of efficiency in the distribution of its progeny which entails the possession of a discriminative faculty of a high order. There is always, even under the most adverse conditions presented in the experiments, a strong tendency for females to deposit only one egg in each host individual thus providing the progeny with the best possible chance of survival. The exercise of this faculty, however, is not perfect, although isolated females in the experiments attained perfection. It is modified by environmental factors, in particular the factors of host and parasite densities per unit area, and there are doubtless others in the natural environment of the parasite which will have the effect of reducing the efficiency which it produces.

Similar results were obtained with *Microbracon hebetor* as described in an earlier paper (Ullyett, 1945). In this case, however, the discriminative faculty was found to be extended to include the ability to judge the size of the host individual in relation to the number of parasite progeny which it can support to maturity. This ability is probably seldom, if ever, required by *Chelonus* and its possession by this species has not been demonstrated. The need for it might occur as between different species of hosts but, even here, the parasite can apparently use a wide range of sizes, all of which are suitable for the progeny. For example, there is a marked difference between the eggs of *Loxostege*, which are approximately the same size as those of *Ephestia*, and eggs of *Heliothis armigera* and *Laphygma* spp. In all cases, the host supports only one parasite individual to maturity so that the faculty would probably never be required by the parasite.

As opposed to this, *Chelonus* females are able to distinguish eggs which are in a suitable stage of development for oviposition. *Microbracon* will use any size of larva although it seems to prefer the larger ones of any species.

The two cases are similar in that the host individual is accessible and immobile at the time when oviposition takes place. It is therefore available for a detailed examination by the female parasite. The distribution of eggs among the available hosts in the two species might therefore be expected to show more or less the same degree of efficiency provided other factors are equal. In the case of *Microbracon* however, the moving host must be found and paralysed first and it was shown (Ullyett *loc. cit.*) that searching and oviposition occurred in two phases of activity. Efficiency deteriorated below a certain host density, a feature which did not occur so markedly with *Chelonus*. This is shown by comparing the frequency distributions showing hosts containing 1, 2, 3,.................... n hosts in each species. In the case of *Microbracon*, the modal group changes as the host density is increased and finally remains stationary as the optimum host density is reached and exceeded; whereas *Chelonus* gives a constant mode throughout the experimental series. *Chelonus* is therefore more efficient in distributing its progeny to best advantage at low host densities than is *Microbracon* and this is apparently due to a greater degree of restraint in oviposition under

adverse conditions as shown by the decrease in total egg production. It should be noted, however, that if more than the optimum number of *Microbracon* progeny are present on a host, they may still all mature but will then give rise to undersized and hence less fecund adults. Thus, size of individuals is sacrificed in favor of numbers where the host density is unfavorable and the effects of competition for food become evident in the parasite population. At the same time, this means that less actual progeny are wasted than would be the case were *Chelonus* to exhibit the same decline in efficiency. Where more than one parasite progeny develops on a host individual, as in the case of *Microbracon*, the faculty of discrimination with an accompanying restraint in oviposition under adverse conditions of host density is therefore not as important as with *Chelonus*, where only one progeny can survive per host.

It is evident that, while a discriminative faculty is highly developed in both species of parasite, it differs in nature and in operation with the fundamental needs of the species. It is adaptable to environmental circumstances and this flexibility, seen particularly in *Microbracon*, tends to offset the adverse effects of unfavorable conditions of host density and the like on the resulting generation of parasites.

Since the discriminative ability of *Chelonus* females is modified by environmental factors, the efficiency of the parasite in the field will vary from time to time and from place to place following continual changes in the nature and intensity of the factors themselves. Two such factors have been studied here, namely, the host/parasite ratio and the parasite density per unit area. These two factors are obviously closely interwoven and will be combined in nature. They will fluctuate together or independently and this will happen in a continuous manner particularly where overlapping of generations occurs to any extent. Since both host and parasite populations are subject to the influence of other environmental factors, many of which are unpredictable (e.g. weather), the results of the fluctuations so produced in nature are also unpredictable except in a very general and qualified manner. No exact outcome of any theoretical postulation regarding the result of parasite efficiency as it will appear in the field is therefore to be expected.

When the main factor present is the parasite density, it is clear that a third factor is produced which affects the efficiency of the parasite. This is the reduction in the total number of eggs per female which occurs with increasing parasite density per unit area. This reduction tends to make each female *apparently* more efficient than would otherwise be the case. Since fewer eggs are laid, there are fewer which have to be satisfactorily placed in hosts and thus the chance of error and consequently of superparasitism in the available hosts is also reduced. Hence any increase in efficiency in the series with varying parasite density may be partially fictitious although it agrees so closely with the single female series.

The problem of parasite efficiency would appear to be divisible into two main phases, viz;

(a) The efficiency of the parasite as a mortality factor in the host population;

(b) its efficiency as related to the maintenance of its own population level within the given area.

These two phases, although related, are distinct and, in part at least, antagonistic. Where the parasite density per unit area remains constant and the host population within that area fluctuates, then the efficiency of the parasite in controlling the host increases with increasing host density until it reaches a maximum. After this point is reached, any further additions to the host popu-

lation result in a small *percentage* of that population being destroyed since the parasite can find and attack only a limited maximum number of hosts per unit of time. Similarly, the number of eggs produced and the efficiency with which they are distributed among the hosts attacked increases with increasing host density until the maximum number which can be laid by the female within the given time is reached. Thus, where parasite density remains unchanged the efficiency of the parasite in both respects is dependent upon the size of the host population.

On the other hand, when parasite density is the variable and where host density per unit area is maintained constant, the outcome is more complicated. Here there is not only a changing parasite population but a progressively changing host/parasite ratio at the same time. As a result of this combination of factors, it is found that, as the parasite density increases,

(1) The total number of hosts attacked and the total number of eggs laid by the entire parasite population increases. This is true up to a point which represents what may be regarded as an optimum parasite density for the given unit of area. Beyond this point, the addition of further parasite individuals causes a decrease in the numbers of hosts attacked and eggs deposited.

(2) The number of hosts attacked per female parasite and the number of eggs laid per female decrease.

(3) The efficiency with which the individual females distribute their eggs among the hosts attacked decreases. This is a direct result of the deteriorating host/parasite ratio and occurs when more than one parasite occupy the unit of area.

An increased efficiency in the control of the host by the parasite population as it grows in numbers and approaches the optimum density for the given area is thus accompanied by a decreased efficiency in the distribution of its progeny and a consequent decline in the proportion of that progeny which will survive to produce adults. Beyond the optimum density, a decrease in number of hosts destroyed occurs as well as a decrease in total egg production. Parasite density, therefore, acts as a factor regulating both the density of the host population of the next generation and the density of its own population.

It is hoped to examine these and other factors limiting the activities and populations of parasites in more detail at a later date. It may be noted here that the host/parasite ratio within a given environmental unit would seem to be one of the main, primary causes of population fluctuations and of population stabilization. Parasite density, with its competition or interference factor, is a secondary cause up to and including the optimum density point, after which it assumes a greater importance as the numbers of parasites per unit area increase. Since the ability to discriminate between suitable and unsuitable hosts would appear to be an attribute common to most hymenopterous parasites (*vide* the work of Salt, 1935; Ullyett, 1936; Lloyd, 1938, 1940 and others), this faculty is basically important but is not fully effective since it is subjected to modification by the host/parasite ratio and by other environmental factors.

## Summary

The effect of host density on the distribution of progeny by single females of *Chelonus texanus* was studied by using varying numbers of eggs of *Ephestia kühniella* per unit area. The efficiency of the parasite in distributing its eggs to best advantage was influenced by the size of the host population but there was always a strong tendency to deposit only one egg in each host. This is shown

by the frequency distribution showing the number of hosts containing 1, 2, 3,............n parasites. The total number of eggs deposited and the proportion of the host population found and attacked by the parasite was dependent upon host density.

The efficiency of the parasite, both in controlling the host population and in maintaining its own population within a given area depends very largely upon the host/parasite ratio. This is emphasized in the experiments in which the effect of increasing parasite density was studied. In these, the host population remained constant and the host/parasite ratio therefore decreased as the number of parasites per unit area increased. An analysis of the results shows that the resulting effect on the efficiency of the parasite was mainly due to the deterioration in the above ratio, and that except at low parasite densities, the effect which can be ascribed to parasite density, as such, is comparatively small. The nature of the data obtained affords evidence of non-random activity in the search of the environment by the parasite.

The implications of the results are briefly discussed as they affect host/-parasite balance in the environment.

A comparison is made with previous experiments in which the distribution of progeny by *Microbracon hebetor* was under examination. It is shown that, while the discriminative ability is highly developed in both species, it differs in nature and degree and is adjusted to the fundamental needs of the species.

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# Description of *Simulium euryadminiculum*, a new species of blackfly (Simuliidae: Diptera)*

*By* D. M. Davies

In material collected from Costello creek in Algonquin Park, Ontario, 1,549 males, 598 females and 2 pupae of a new species of blackfly were encountered. This species was present in material which was collected daily during the spring and summer of the years 1938-1943 using a cubic yard screen cage placed over the stream.

This species began to emerge between May 7 and 23 in most years, but the total number of flies was smaller when emergence began by May 10 than when it began on May 17 or later. The only exception to this occurred in 1938 when emergence began earlier and continued over a much longer period than usual. The main portion of the emergence ended between May 10 and 29 although occasional flies emerged as late as June 18. None of the new species was collected in 1942. Association of males and females of the new species was possible as both sexes emerged during the same period and as other species, emerging at the same time, were readily identified in both sexes.

Two pupae were found in this material from one of which the adult male genitalia were dissected and mounted in balsam.

## Description of Adult

The descriptions are based on the type specimens preserved in 95% alcohol and in balsam slide mounts.

*Female*: length 2.8 mm., wing length 3.0 mm.

Head: dichoptic eyes; dark brown with mouthparts light brown; front and clypeus dark brown with fine silvery pilosity, the former tapering slightly below, at its narrowest point half the width of clypeus; clypeus as broad as long; antennae eleven-jointed (Fig. 1a) unicolorous, elliptical in section, third joint twice the length of all but the terminal joint; palpi as long as antennae, third joint being conspicuously darker than the others.

Thorax: scutum shining dark blackish-brown with fine silvery uniform pilosity with a few longer hairs posteriorly; scutellum, from pale to dark brown with longer brownish-golden hairs; pleural and sternal plates shining, hairless except for long golden hairs on subalar epipleurites and upper quarter of mesepimera; postnotum hairless and shiny. Wings: hairs on costa and on dorsal surface of radius distal to radio-medial crossvein intermixed with spinules; subcosta with a single dorsal row of 16 hairs; radius with hairs proximal to crossvein; radial sector simple, hairy ventrally, a single dorsal row of hairs; hairs on stem vein and proximal end of costa, pale; second basal cell small but distinct in eight flies, partly developed in two others (Figs. 2a, b), tiny sense pores most common at base of veins; halteres white with base of stalk dark brown. Legs: (Fig. 3a) yellowish to light brown with dark brown markings at the joints and the fore- and mid-tarsi and the two terminal joints of the hind-tarsi dark brown, pilosity mainly pale, with more brown hairs on tarsi; hind basitrsus 1.5.2, two thirds width of tibia; calcipala and pedisulcus well-defined; claws with large obtuse tooth.

Abdomen: pilosity including basal fringe pale yellow to silvery, hairs mostly appressed, thicker on the sides; tergal plates of segments 3-4 greatly reduced and 5-6 partly reduced; sternites except the eighth membranous, tergal plates

*Contribution of the Department of Zoology, University of Toronto and the Department of Parasitology, Ontario Research Foundation.

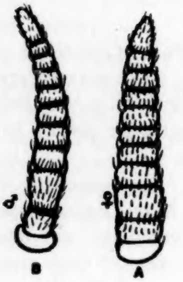


FIG. 1

*The left antenna*
*A female B male*


FIG. 2

*The second basal cell of the wing*
*A, B female C male*


FIG. 3

*The left hind leg*
*(ventral view)*
*A female B male*

and dorsal surface light to dark brown becoming yellow to grayish-yellow ventrally. Genitalia: (Figs. 4a,b) ovipositor valves membranous, inner margin thinly sclerotized, truncate, wider than long; anal lobe as long as cercus, subquadrate, more pointed dorso-posteriorly, setose posteriorly, more sclerotized anteriorly; cercus rounded distally; arms of genital rod spreading, each expanded into a quadrangular plate bearing a large sclerotized tooth on its outer margin and terminating in a less sclerotized portion.

*Male*: length 3.4 mm., wing length 3.2 mm.

Head: holoptic eyes much larger than those of female, the area of larger eye facets showing up redder than the ventral area; third joint of antenna longer than that of female and than all other joints (Fig. 1b).

Thorax: similar to that of female but hairs on subalar epipleurites and mesepimera dark brown. Wings: subcosta bare, hairs on stem vein and proximal end of costa dark; second basal cell absent in five flies, partially formed in five others (Fig. 2c); halteres light brown to orange, base of stalk dark brown. Legs: (Fig. 3b) as in female but pilosity darker and more spreading; hind basitarsus wider than that of female, 1:3.6 and two-thirds width of tibia.

Abdomen: soft parts yellow to light brown, sclerotized portions dark brown to blackish-brown, hairs including basal fringe dark brown, not appressed, sparse on the sides; tergal plates not reduced, small sclerotized sternal plates on segments 3-8. Genitalia: (Figs. 5a,b,c) side piece as long as wide, quadrate, narrower dorsally; clasper longer than wide 1:2.5, one third as long again as side piece, flat ellipse in section, from the side a tapering sharply-pointed hook, ventrally slowly tapering to an obtuse end with a single small tooth, a weak elbow halfway up clasper from latero-ventral aspect; adminiculum wide, thin, glassy, transparent, expanded portion 1:1.7 covered with fine hairs in the centre, basal prongs barely S-shaped, incurved slightly at the tips; adminicular arms with teeth and fimbriae intermixed, posteriorly angled, spreading anteriorly.

**Description of Pupa**

Pupa: length, female 2.9 mm., male 3.1 mm.; filaments 3.4 mm., 4 filaments arranged in pairs, dorsal pair supported by a shorter, stouter stalk (Fig. 6); spines

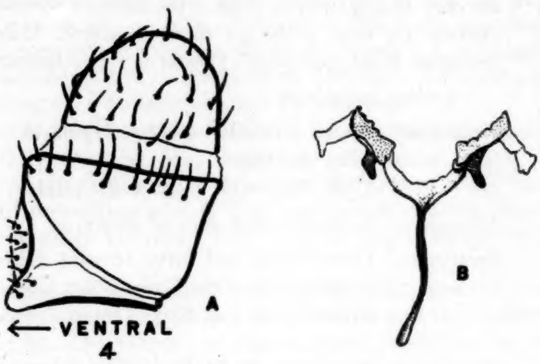


FIG. 4

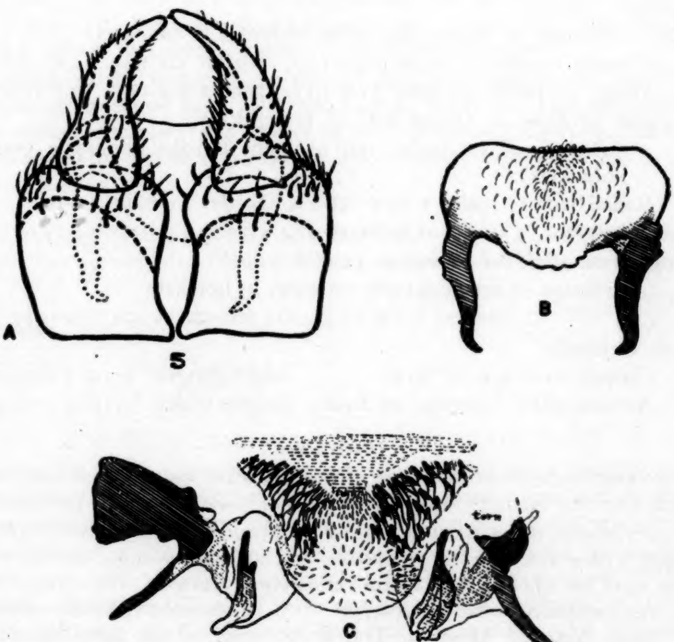


FIG. 5

*Genitalia: 4A anal lobe and cercus; B genital rod (v); 5A side piece and clasper (v); B adminiculum (v); C adminicular arms (d), right side torn and folded (v = ventral; d = dorsal)*


FIG 6
*The pupil filaments (right side)*

on abdominal segments including ninth but no terminal spines; cocoon closely woven with a thickened anterior margin, female cocoon 2.9 mm., male 3.3 mm. in length. Male genitalia were dissected from one pupa; clasper 1:2.3; adminiculum 1:2.0.

Larva: unknown.

Holotype: Male, Costello creek, Algonquin Park, Ontario, May 20, 1940 (F.P. Ide) Can. Nat. Coll. (slide).

Allotype: Female, other data as above.

Paratypes: Forty males and forty females, other data as above; to be placed in the Canad. Nat. Coll., U.S. Nat. Mus., British Mus. and Roy. Ontario Mus.

**Variations from the Adult Type Characters**

A series of flies was examined to determine the range in variation and the average size and shape of several characters which were considered of systematic importance.

*Size*: (average of fifteen flies with extremes in brackets)

Length: males 3.1 mm. (2.9-3.7); females 3.2 mm. (2.8-3.5)
Wing: males 3.0 mm. (2.8-3.3); females 3.3 mm. (3.0-3.6)

*Number of hairs on Dorsal Side of Wing Veins:*

(average of six males and of eight females with the extremes in brackets).

Radial Sector: males 1 hair (0-2); females 5 hairs (2-10)
Subcosta: males 0 hairs (0-1); females 14 hairs (4-22)

*Proportions of Hind Basitarsus (width/length)*

(average of ten flies with extremes in brackets

males: 1:3.8 (3.4-4.1); females: 1:5.3 (5.0-5.8)

*Male Genitalia*

Clasper (average of five) width/length: 1:2.6 (2.5-2.9)
Adminiculum (average of four) length/width: 1:1.8 (1.7-1.9)

**Discussion**

A comparison with descriptions of neartic, neotropical and British blackflies, indicated that this blackfly was different from those described previously.

*S. euryadminiculum* is most similar to *Simulium canonicolum* (Dyar and Shannon). There are only three females of the latter species, which were collected in 1922 by H. G. Dyar from Yellowstone Canyon, Wyoming. The new species was compared with a paratype of *S. canonicolum*, kindly sent by the United States National Museum. The proportions of the hind basitarsus in a balsam mount are 1:5.3 (5.0-5.8) in the former and 1:6.1 in the latter. Specimens of *S. euryadminiculum* preserved in alcohol, were dried to compare with *S. canonicolum*. The integument of the latter is a reddish-black, whereas in the former it is a dark blackish-brown. Two paler areas are present on the antero-lateral portions of *S. canonicolum* which are lacking in the new species. The occiput and the ventral end of the clypeus are hairier than in *S. euryadminiculum*. The tergal abdominal plates are more reduced than in the new species. The genital rod of *S. canonicolum*, as drawn by Dyar and Shannon (1), is dissimilar to that of the new species, spreading less posteriorly.

The females of *Cnephia borealis* (Malloch) might be confused with those of *S. euryadminiculum.* However, there is no tuft of pile on the mesopleural membrane in the new species as in *C. borealis.* The hind basitarsal proportions are even farther removed from the new species being 1:7 and there is neither a calcipala nor pedisulcus in *C. borealis.* The difference between the adminicula is sufficient to separate the males of these two species.

The females of *Simulium pugetense* (Dyar and Shannon) resemble this new species superficially but the hind basitarsal proportions are greater and are described by Twinn (3) as 1:7.5 although in the present study some specimens were found with proportion of 1:6. The anal lobe in the new species is as long as the cercus whereas in *pugetense* it is twice as long. The genital rods are also distinctly different.

The new species has been placed in the genus *Simulium* following the classification of Smart (2), since the pedisulcus is distinct and the cocoon is definitely thickened at the lip. The number of macrotrichia (hairs) on the upper surface of the distal end of the radial sector in a series of males was 0,0,1,1,1,2 (+ 1 spinule) and in a series of females 2,2,3,3,6,6,9,10, although in a few cases it was difficult to determine whether a hair was on the radial sector or the costa. These hairs are present in *Cnephia* whereas in *Simulium* they may be present or absent. As shown above, the hairs are absent in some male wings and in the others very few, which brings this species closer to the genus *Simulium.*

In examining the wings of ten flies of each sex, variation in the condition of the basal cell (second basal cell) was found (Table 1). This variation in the basal cell taken alone places the species midway between the two genera *Cnephia* and *Simulium.* This species is possibly a link between the two genera.

TABLE I

*Extent of Development of Second Basal Cell in the Wing of S. euryadminiculum.*

| Basal Cell | Complete | Partial | Absent |
|---|---|---|---|
| Male | 0 | 5 | 5 |
| Female | 8 | 2 | 0 |
| | 8 | 7 | 5 |

The species name *euryadminiculum* was proposed since one of the most striking characters is the wide adminiculum; *eury* means wide and *adminiculum* means a supporting or auxiliary piece (from the Latin ad=to add, manus=hand).

I am grateful to the University of Toronto for giving me the opportunity to do this work and especially to Professor F. P. Ide, Department of Zoology, under whose direction the work was carried out. I am indebted to Dr. H. B. Speakman, Director of the Ontario Research Foundation, for providing the means and facilities to accomplish this research and I wish to thank Dr. A. M. Fallis, Director of the Department of Parasitology, Ontario Research Foundation, for his helpful advice.

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# On a Migration of *Tarnetrum corruptum* (Hagen) (Odonata) in Western Oregon

*By* Ralph W. Macy
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On the warm afternoon of August 29, 1948, as I was walking through a wheat stubble-field on my farm located six miles southwest of McMinnville, Oregon, I became aware that I was in the midst of a dragonfly migration. I could see them all about me for a radius of perhaps seventy-five feet which was about the limit of my vision for an insect of this size. When first seen there was a considerable number passing toward the west with from thirty-five to fifty of the insects visible at any given moment but after about five minutes they began to thin out until only a few were visible. I then walked south for two hundred feet at which place another heavy concentration was encountered. After a short interval these thinned to a few stragglers. Thinking that the migration was about over I retraced my steps only to meet with another wave. It soon became apparent that the migration was taking place over a wide front and that the insects tended to fly in groups over the valley floor.

To the east, from which the dragonflies were coming, the nearest water is the South Yamhill River, about two miles distant, but there is no reason to believe that this stream was their point of origin. Except for several rivers these migrants could have crossed some fifty miles of dry fields before reaching this area which lies at the edge of the foothills of the Coast Mountains.

A deep ditch bordered by clumps of willows lay directly across the path of the insects and within twenty to fifty feet of this they began to rise in order to clear the shrubbery. Otherwise they flew at a height ranging from two to ten feet above ground with a few travelling higher. Their average speed was estimated to be from four to five miles per hour as long as the breeze into which they were flying remained gentle.

As far to the north as a quarter of a mile the migration continued but with fewer participants perhaps due to the fact that this region was on a hillside some two or three hundred feet above the valley. As a heavy sea breeze began to surge from the west the speed of the flight was somewhat slowed and the insects in some instances came to within several inches of the ground but in no case did a single one turn back, alight, nor deviate from a westerly course. Near the top of the hill these insects were passing at the rate of seven per minute over a fifty foot front.

At the height of the migration, when first observed at 2 p.m., the temperature was approximately 80°F whereas by four o'clock it had become considerably cooler but the migration continued unabated. Unfortunately I was unable to continue my observation for several days thereafter so that the duration of the flight is unknown. On the night of September 4, a single specimen of the migrant came to the lighted window of the house on the farm and was caught. This suggests the interesting possibility of night flight, also observed at times in butterfly migrations, but it is also quite possible that the dragonfly had been aroused from a nearby resting place. Careful search in the vicinity on the following days did not reveal any additional specimens.

Because the migrants were abundant during the migration and without exception were flying in one direction at a moderate speed it appeared that many might be taken in a few minutes. However this turned out to be an illusion, for all but two of the insects managed to elude me during an hour of determined

effort with the net. One of the two which I captured was very kindly identified by Dr. E. M. Walker of the Royal Ontario Museum of Zoology in Toronto as *Tarnetrum corruptum* (Hagen), until recently placed in the genus *Sympetrum*. Dr. Walker commented that the species has the reputation of being a wanderer.

Another dragonfly, determined by Dr. Walker as *Sympetrum pallipes* (Hagen), was rather common in the vicinity of the migration but its flight behaviour was entirely different for after flying about at random for a few minutes it always stopped to perch whereas the migrant flew steadily in one direction and not one ever alighted.

## Important Advances in Zoological Nomenclature Achieved at the Thirteenth International Congress of Zoology, Paris, July, 1948

During the Thirteenth International Congress of Zoology which closed at Paris on Tuesday, 27th July, the International Commission on Zoological Nomenclature, holding its first meeting since the close of the war, put forward a comprehensive programme for the reform and development of Zoological Nomenclature.

Measures taken to reform procedures are designed to enable the Commission to reach decisions much more rapidly than has been possible in the past.

Reforms were agreed upon which, while retaining everything in the International Rules that experience has shown to be valuable, will eliminate all those passages which have been found to be unsatisfactory and meet the needs of zoologists by the introduction of provisions on matters which have hitherto not been subject to international regulation.

Decision was also reached to modify the international law on zoological nomenclature by incorporating in the Rules themselves the decisions hitherto embodied only in the "Opinions" of the Commission.

It is hoped that as a result of the decisions taken at Paris workers giving new names will, from now onwards, have at their disposal rules which are simple, clear and easy to operate. In the matter of names already published it is planned to extend the "Official List" of generic names in Zoology, for under the arrangements now agreed upon, a name once placed on this list is not to be changed for any purely nomenclatorial (as contrasted with taxonomic) reason without the prior approval of the International Commission. A similar provision has been made in regard to the trivial names of species. The establishment of these two "Official Lists" makes it possible for specialists in any group to concert proposals for submission to the Commission for the insertion in these "Official Lists" of the names of the genera and species in their group and thereby to protect those names from changes for any reason other than taxonomic considerations.

The effect of the reforms in the Rules instituted during the Paris meeting will be to provide zoologists with a system of law which will be much easier to operate and will ensure stability and uniformity in zoological nomenclature. At the same time reforms in the constitution of the Commission and its procedure will assure to zoologists a central authority in regard to all matters relating to zoological nomenclature far more representative and international than ever before and, as such, capable of providing a service more extensive and of much greater value than has been possible at any previous time.

J. R. Dymond,
*Royal Ontario Museum of Zoology.*

## The Red-Legged Ham Beetle on Imported Copra

*By* W. W. JUDD
McMaster University, Hamilton, Ont.

On July 19, 1947 an investigation was madé, on behalf of the Department of Health of the City of Hamilton, of the occurrence of the red-legged ham beetle, *Necrobia rufipes* DeGeer (Cleridae), in the warehouse of a company manufacturing vegetable oils in Hamilton, Ontario. The beetles were found in large numbers in a shipment of copra from the Philippine Islands. Larvae were attacking the broken coconut but were the cause of little concern to the manufacturer since the copra was used for making oils, and the residue for feed for stock. However, the adults were invading houses adjacent to the warehouse, causing a nuisance to housewives. The occurrence of the beetles attracted the attention of the local press[1].

About fifty adult specimens were captured for examination and were identified with the aid of keys of Blatchley[2] and Patton[3]. Pinned and preserved specimens have been deposited in collections at McMaster University. On July 28 four more specimens were received. They had been found in a railway yard about three miles from the warehouse and it was reported that they nipped the skin sharply when disturbed.

The beetles and larvae were not considered to be injurious to the copra and no measures were taken for their control. The infestation died out as the copra was used.

1. The Hamilton Spectator, Aug. 9, 1947.
2. Blatchley, W. S. 1910 Coleoptera or beetles known to occur in Indiana. Nature Pub. Go., Indianapolis, Indiana.
3. Patton, W. S. 1931 Insects, ticks, mites and venomous animals of medical and veterinary importance. Part 2. H. R. Grubb, Ltd., Croydon, England.

## A Method of Keeping Paradichlorobenzene in Insect Boxes*

*By* WM. L. PUTMAN
Dominion Fruit Insect Laboratory, Vineland Station, Ont.

Keeping a supply of paradichlorobenezene or naphthalene in insect boxes for protection against dermestids has always been a problem. Small cloth bags or wire screen boxes are frequently used but are a nuisance to fill and require several pins to hold them in place. The method used for protecting the collections at the Vineland Station Laboratory appears to be more convenient.

Rolls of dental cotton, which are about three-quarters of an inch in diameter, are cut into pieces two inches long and mounted crosswise on ordinary office pins. Paradichlorobenzene is melted (M.P. 53° C.), most conveniently in a can placed in a vessel of hot water, and the pieces of cotton are dipped into it. The cotton becomes saturated almost instantaneously and is laid on a board until the paradichlorobenzene solidifies.

When the pieces are put into an insect box the pin should be pressed into the cork at an angle so that the cotton rests firmly on the bottom. The paradichlorobenzene will eventually evaporate, but the old pieces of cotton can be easily replaced by freshly dipped ones and the exhausted pieces redipped and used indefinitely. The boxes should be examined and the paradichlorobeneze renewed at least twice a year.

*Contribution No. 2598, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada.

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